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19 **Keywords** phenotypic flexibility; phenotypic plasticity; intra-specific variation in social
20 organization; alternative reproductive tactic; extrinsic factors; environmental disrupters;

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23

24

25 **Abstract**

26 Many species show intra-specific variation in their social organization (IVSO), which means
27 the composition of their social groups can change between solitary living, pair-living or living
28 in groups. Understanding IVSO is important because it demonstrates species resilience to
29 environmental change and can help us to study ultimate and proximate reasons for group-
30 living by comparing solitary and group-living individuals in a single species. It has long been
31 realized that the environment plays a key role in explaining the occurrence of IVSO. IVSO is
32 expected to have evolved in variable environments and can thus be a key adaptation to
33 environmental change. It has previously been shown that four different mechanisms relying
34 on the environment exist that can lead to IVSO: environmental disrupters, genetic
35 differentiation, developmental plasticity, and social flexibility. All four mechanisms depend
36 on the environment such that focusing only on environmental factors alone cannot explain
37 IVSO. Importantly, only three represent evolved mechanisms, while environmental disrupters
38 leading to the death of important group members induce non-adaptive IVSO. Environmental
39 disrupters can be expected to cause IVSO even in species where IVSO is also an adaptive
40 response. Here we focus on the questions of why IVSO occurs and why it evolved. To
41 understand IVSO at the species level it is important to conduct continuous long-term studies
42 to differentiate between non-adaptive and adaptive IVSO. We predict that IVSO evolves in
43 environments that vary in important ecological variables, such as rainfall, food availability,
44 and population density. IVSO might also depend on life history factors, especially longevity.
45 IVSO is predicted to be more common in species with a short lifespan and that breed only for
46 one breeding season, being selected to respond optimally to the prevailing environmental
47 situation. Finally, we emphasise the importance of accounting for IVSO when studying social
48 evolution, especially in comparative studies, since not every species can be assigned to one
49 single form of social organization. For such comparative studies, it is important to have
50 reliable data-bases based on the primary literature.

51 **Introduction**

52 Formerly, it was assumed that every species has a specific social system and deviations from
53 it were regarded as abnormal or noise. However, it has been recognized that each of the three
54 components of a species social system (Kappeler & Schaik 2002) can vary within the species
55 (Lott 1984; Lott 1991): i.e. its mating system (who mates with whom), its social structure
56 (how individuals interact with each other), and its social organization (whether they are
57 solitary, pair-living or living in groups of different composition). Most information is
58 available for the social organization of species. The social organization can affect the social
59 structure and the mating system, influencing the entire social system.

60 Intra-specific variation in social organization (IVSO) during breeding occurs when a
61 species shows two or more of the following forms of social organization (Lott 1991; Schradin
62 2013): living solitarily, in pairs, one breeding male with several breeding females, one
63 breeding female with several breeding males, or multi-male multi-female groups. Each form
64 of social organization must be composed of breeding individuals, not only dispersing solitary
65 individuals or bachelor groups. Variation in group-size and optimal group size are important
66 topics in behavioral ecology (Markham & Gesquiere 2017), but, following our definition, do
67 not indicate IVSO if the relative numbers of breeders of each sex does not change.

68 IVSO occurs in several taxa, including insects and vertebrates. For example, burying
69 beetles (*Nicrophorus vespilloides*) can be solitary, form pairs or communal groups with two
70 or more breeding females (Eggert 1992), depending on the size of the carrion for which they
71 compete, with more beetles associating at larger carrion (Müller et al. 2006). Similarly, pied
72 kingfishers (*Ceryle rudis*) can live in pairs, in family groups with philopatric adult offspring,
73 or in polygynous groups, depending on the availability of good nesting sites (Reyer 1980;
74 Reyer 1984). The house mouse (*Mus musculus*) can live solitarily, in pairs or in communal
75 groups, with resource availability modifying the intensity of intra-specific competition (intra-
76 sexual aggression in males and female infanticide) (Latham & Mason 2004; Berry et al. 2008).

77 Dunnocks (*Prunella modularis*) also show varying forms of social organization to maximize
78 individual fitness (Davies 1992), which was used as a model system to study the evolution of
79 sexual conflict, mating systems, parental effort and life histories (Burke et al. 1989; Davies et
80 al. 1996). Male and female dunnocks can change their mating system (monandry, polygyny
81 and polyandry) and social organization (pairs, one female and several males, or multi male
82 multi female groups). In a series of sophisticated experiments, including measuring individual
83 fitness, it was demonstrated that IVSO is the consequence of individual dunnocks choosing
84 the reproductive tactic with the highest fitness depending on the prevailing ecological
85 conditions (Davies 1992).

86 To understand IVSO, it is not sufficient to study the related environmental factors.
87 Tinbergen proposed in his four questions that behavior must be understood from the
88 perspectives of ontogeny, causation, phylogeny and function (Tinbergen 1963), and the
89 environment plays a crucial role in all four questions (Schradin 2018). Physiological
90 mechanisms are evolved traits (Hofmann et al. 2014) and thus to understand why IVSO
91 evolved, one must understand the mechanisms leading to IVSO. Thus, the first step to
92 understand why IVSO occurs is to describe and differentiate the mechanisms of IVSO.

93 After summarizing a previous review on IVSO (Schradin 2013), we outline three
94 important new aspects. First, we show the importance of differentiating between adaptive and
95 non-adaptive IVSO. Second, we focus on the questions of why IVSO occurs and why it
96 evolved. Third, we show the importance of accounting for IVSO when studying social
97 evolution, particularly in comparative studies. Finally, we summarise hypotheses and
98 predications about the evolution of IVSO. Our major aim is thus to encourage more research
99 on evolutionary reasons of IVSO and to emphasise the importance of considering IVSO in
100 comparative studies.

101

102

103 **The four mechanisms that can lead to IVSO**

104 In a 2013 review, Schradin proposed four different mechanisms that can lead to IVSO, each
105 mechanism depending on environmental factors (Schradin 2013): environmental disrupters
106 (entirely extrinsic factors), genetic differentiation, developmental plasticity, and social
107 flexibility. Environmental disrupters occur when natural mortality due to old age or predation
108 changes the social organization, which represents a non-adaptive change imposed on the
109 group. IVSO is thus not caused by the remaining individuals which will respond to this new
110 situation with adaptive tactics. This is discussed in detail below. Genetic differentiation refers
111 to the possibility that sub-populations of one species might differ genetically which could
112 influence the resulting social organization. By genetic differences we refer to heritable
113 differences of the genome (for behavior see (Hu & Hoekstra 2017) for social behaviors
114 (Bendesky et al. 2017); (Dochtermann et al. 2015), which includes not only differences in
115 genes and alleles, but also differences in genomic regions that regulate gene expression.
116 However, while genetic differences between populations of the same species could explain
117 the occurrence of IVSO, evidence for this process is rare to absent. The best example could be
118 fire ants (*Solenopsis invicta*) which have two social forms (polygynous with several breeding
119 females and monogynous with one breeding female) and it is a single polymorphism at the
120 locus Gp-9 that determines the social organization of a colony. Queens that are homozygous
121 BB at this locus attempt to found a colony alone, while Bb and bb queens do not fly far but
122 attempt to join a colony (Gotzek & Ross 2007; Gotzek & Ross 2009; Keller 2009; Ometto et
123 al. 2011). Future studies might reveal more examples where genetic differentiation could
124 explain IVSO, but to date empirical evidence does not indicate that it is a common
125 mechanism of IVSO.

126 IVSO can be caused by phenotypic plasticity. Non-reversible phenotypic plasticity is
127 called developmental plasticity, depending on organizational effects during early development
128 (Phoenix et al. 1959; West-Eberhard 2003) or puberty (Zimmermann et al. 2017). In

129 developmental plasticity, the environment determines which one of two or more alternative
130 phenotypes develops. If the social behavioral phenotype is permanently influenced during
131 early development, the social organization of this population could differ either from
132 generation to generation, or compared to another population, in both cases leading to IVSO.
133 However, to date there is no empirical evidence that developmental plasticity causes IVSO;
134 yet, future studies might reveal species in which developmental plasticity causes IVSO.

135 Social flexibility, i.e. reversible phenotypic plasticity (Piersma & Drent 2003) of
136 individual social tactics, is the best empirically documented mechanism leading to IVSO.
137 Flexibility in social behavior is common, because individuals have to respond flexibly
138 depending on the social situation. In primates, flexible dominance hierarchies enable
139 individuals to cope with conflict, enabling them to remain in their group even if new conflict
140 arises (Judge 2000). This is an important social ability in many obligatory group-living
141 species, in which living solitarily is very costly and leads to increased mortality. Individuals'
142 flexibility in social behavior stabilizes the social system including the social organization of
143 the species, which can explain why social organization in primates is very stable (Shultz et al.
144 2011). In social species where individuals are less flexible in their social response, alternative
145 and reversible social tactics might exist. Therefore, social flexibility leading to IVSO might be
146 particularly common in species with low flexibility in social behavior, while flexibility in
147 social behavior can maintain the existing social organization. Flexibility in social tactics in
148 both sexes can change the social organization of the entire population. This mechanism is
149 called social flexibility (Schradin et al. 2012) and has been shown to cause IVSO in burying
150 beetles (Eggert 1992; Müller et al. 2006), pied kingfishers (Reyer 1980; Reyer 1984), house
151 mice (Latham & Mason 2004; Berry et al. 2008), great gerbil (*Rhombomys opimus*; (Randall
152 et al. 2005) and African striped mice (*Rhabdomys pumilio*; Schradin et al. 2012).

153 Schradin (2013) identified that for all four possible mechanisms, the environment
154 plays a critical role. Thus, to understand which mechanism is at play, it is not sufficient to

155 study the environmental factors. One must also establish whether the underlying physiological
156 mechanisms are genetically determined, organizational, or activational (Table 2 in Schradin,
157 2013). In accordance with Piersma & Gils (2011), Schradin (2013; Table 2) hypothesized that
158 the predictability of the environment will determine which mechanism evolved such that: (i)
159 genetic differentiation evolves in predictable environments (two or more populations with
160 different but predictable environments); (ii) developmental plasticity occurs in short-term,
161 predictable environments (the individual can predict from the environment in which it grows
162 up the environment in which it will breed); and (iii) social flexibility evolves in unpredictable
163 environments. As environmental disrupters do not represent an evolved mechanism of IVSO,
164 it is also not associated to a specific physiological mechanisms nor a specific environment
165 (Schradin 2013).

166

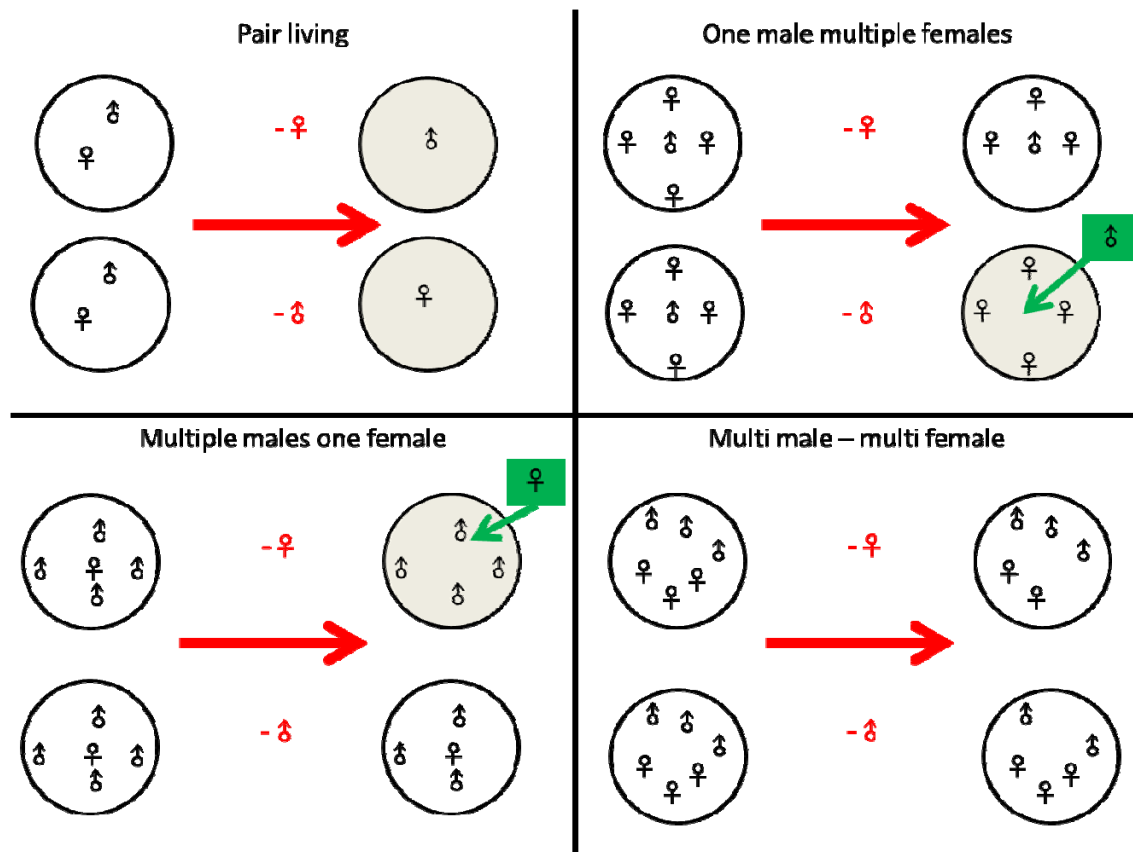
167 **How to recognize the different mechanisms?**

168 Schradin (2013) identified two questions one needs to answer to show which one of the four
169 mechanisms explains an observed IVSO (Table 3 and 4 in Schradin 2013). 1. Does IVSO
170 occur within or between individuals? This differentiates between genetic variation and
171 developmental plasticity (IVSO between individuals) on the one hand and entirely extrinsic
172 factors and social flexibility on the other (IVSO occurs within individuals). 2. If IVSO occurs
173 between individuals, to differentiate between genetic variation and developmental plasticity
174 one would have to answer the question ‘to what extent does the genotype or the environment
175 determine the social tactics shown by individuals? If IVSO occurs within individuals, one has
176 to (i) establish whether the environment induces changes in individual behavior which in turn,
177 leads to a new form of social organization (social flexibility), or (ii) whether the social
178 organization is changed due to one (or more) individuals disappearing (environmental
179 disrupters).

180

181 **IVSO can be non-adaptive**

182 Environmental disrupters are common reasons of IVSO but do not represent an adaptation,
183 but a case where a change in social organization is imposed on the individuals by the
184 environment. If an important group member dies, the social organization of the entire group
185 might change (Fig. 1). For example, in pair-living species, if one of the two breeders dies, the
186 other individual automatically becomes solitary living (Fig. 1). The death of a single
187 individual in pair-living Scandinavian wolves often results in temporarily solitary individuals
188 (Milleret et al. 2017). Individuals might then respond adaptively to this imposed change, such
189 as by re-pairing as reported in beavers (*Castor fiber*; (Mayer et al. 2017). In pair-living
190 species where the offspring remain in their natal family after reaching adulthood and help in
191 raising their younger siblings, the death of one of the two breeders often leads to reproductive
192 conflicts between the adult non-breeders, which can lead to several forms of social
193 organization. For example, cooperatively breeding callitrichid primates reportedly show
194 considerable IVSO, which has been typically interpreted as an adaptive strategy (Garber 1997;
195 Garber et al. 2016). However, IVSO in callitrichids is often induced by the disappearance of a
196 dominant breeder, for example a breeding male in Goeldi's monkeys (*Callimico goeldii*)
197 (Porter et al. 2001), in black faced lion tamarins (*Leontopithecus caissara*) (Martins et al.
198 2015), or in mustached tamarins (*Saguinus mystax*) (Löttker et al. 2007). In these examples,
199 the changes in social behavior observed in the remaining individuals can be regarded as
200 adaptive, since each individual attempted to optimize its fitness under the new social
201 conditions and to obtain a breeding position. However, the observed IVSO itself was not
202 caused by the individuals. IVSO due to environmental disrupters therefore seems to be very
203 common.



204

205 **Fig. 1**

206 Mortality of a single individual (indicated by a red arrow and red sex specific symbol) can change the
 207 social organization if there is no other breeding individual of the same sex in the group (indicated in
 208 grey). This is especially the case in pair-living species (top left), but not in species living in multi-male
 209 multi-female groups (bottom right). In species where groups typically consist of only one individual of
 210 one sex and multiple individuals of the other sex, mortality of only the individual of the rarer sex
 211 changes the social organization (one male multi female groups top right, and multiple males one
 212 female groups bottom left). However, in these species, often the vacant breeding position is taken over
 213 very quickly (for example from males in bachelor groups), such that no IVSO might be observed
 214 (green insets). Note that pair-living species often have groups that also contain adult non-breeders,
 215 for example in cooperatively breeding species such as wolves and callitrichids. In these species, mortality
 216 of a dominant breeder typically leads to conflict between the remaining group members about who
 217 will become a breeder.
 218

219 It is important to know whether the observed IVSO is due to an environmental
 220 disrupter or due to the adaptive choice of individuals. In facultative group-living African
 221 striped mice, solitary breeding in females has been described as an adaptive tactic to avoid
 222 reproductive competition within groups (Schradin et al. 2010). However, long-term studies
 223 revealed that solitary breeding in female striped mice could be the result of two alternative

224 mechanisms: 1. females leaving the communal group to become solitary breeders, indicating
225 an individual choice; or 2. females becoming solitary breeders because all other females of
226 their group have disappeared, probably due to predation (Hill et al. 2015a). This difference in
227 mechanisms is also represented in differences between females, with solitary females that left
228 the group having a higher body mass and lower corticosterone levels than females that
229 remained in the group, whereas females that became solitary due to environmental disrupters
230 did not differ from group-living females in body size or hormonally (Hill et al. 2015a; Hill et
231 al. 2015b). However, females that chose to become solitary differed significantly in body
232 mass and in hormone levels from females that became solitary due to environmental
233 disrupters (Hill et al. 2015a; Hill et al. 2015b). Thus, to understand the proximate mechanisms
234 and ultimate consequences of solitary breeding, it is important to know whether solitary
235 breeding has been caused by an environmental disrupter or by adaptive individual choices.

236

237 **The importance of long—term field studies with continuous monitoring**

238 Identifying IVSO is challenging, especially for long-lived species. It requires long-term field
239 studies (Hayes & Schradin 2017) which are difficult to initiate and sustain (Schradin & Hayes
240 2017). The history of the group must be known for an extended period of time to identify
241 whether changes in social organization are the result of individual choices, indicating adaptive
242 IVSO, or due to environmental disrupters changing the group organization. Thus, long-term
243 field studies must contain continuous observations over several years, not just several
244 extended field trips to the same field site over a few years. This is in contrast to many projects,
245 which are typically funded for only three years, with periods between study years when no
246 field data are collected, and when important members of the study population might disappear
247 for then unknown reasons (Porter et al. 2001). While it is easy to provide adaptive
248 interpretations to explain the observed IVSO, whether or not it is really adaptive or the
249 consequence of environmental disrupters remains unknown. It is important to be aware that

250 cases of non-adaptive IVSO due to environmental disrupters can also occur in species where
251 adaptive IVSO occurs, as was demonstrated in the case of solitary breeding in African striped
252 mice (Hill et al. 2015b).

253

254 **Why did IVSO evolve?**

255 Regarding the evolution of IVSO, one can ask several questions. 1. Which environmental
256 factors lead to the evolution of IVSO? 2. How do environmental factors differ between the
257 three described adaptive mechanisms? 3. Which life history traits are related to the evolution
258 of IVSO?

259 IVSO may represent an adaptive response to spatio-temporal variation in
260 environmental conditions (Table 1). Accordingly, stable social organizations can be expected
261 in stable or predictable environments. Such social stability is beneficial because all forms of
262 phenotypic plasticity have costs such as gathering the correct information to decide which
263 phenotype to develop, costs of nervous system tissue to make fitness-enhancing decisions
264 (e.g., dispersal vs. natal philopatry), the risk of developing the wrong phenotype, and the time
265 cost to change (for reviews see (VanBuskirk & Steiner 2009; Auld et al. 2010; Piersma & Gils
266 2011). To avoid these costs, having a stable social organization might be the optimal solution
267 for species evolving in stable or predictable environments. However, if the costs and benefits
268 of social stability differ between sexes (Ebensperger et al. 2016), inter-sexual conflict could
269 facilitate changes in social organization within populations. IVSO might be expected in
270 species that have large geographical ranges encompassing very different environments.
271 Variation in ecological conditions between populations could lead to genetic differentiation
272 affecting the social system and thus IVSO between populations. This could be the starting
273 point of speciation (Meynard et al. 2012; Rymer et al. 2013; Nonaka et al. 2015).

274 Adaptive phenotypic plasticity within populations, including IVSO, can evolve in
275 environments that are variable (Table 1). For an adaptive response to evolve, this variation

276 must be repeatable in different generations. For example, IVSO could evolve in environments
 277 characterized by repeated, predictable environmental disrupters resulting in periods of high
 278 and low availability of resources, such as periodic El Niño-Southern Oscillation (ENSO)
 279 events (Zabel & Taggart 1989; Dickman et al. 2010). Any given ENSO cannot be predicted
 280 precisely, but it is predictable that ENSO will occur again in the future. Thus, animals that
 281 evolved in areas where ENSOs occur experience periodic but predictable variation, to which
 282 IVSO could be an adaptation (Zabel & Taggart 1989; Dickman et al. 2010).

283 Variation in population density may drive IVSO as it influences the availability of
 284 breeding territories (habitat saturation hypothesis: (Emlen 1982; Koenig et al. 1992). For
 285 example, the social organization of striped mice in the Succulent Karoo is mainly dependent
 286 on population density, with solitary living occurring in generations experiencing low
 287 population density and communal breeding in generations experiencing high population
 288 density (Schradin et al. 2010). Whether developmental plasticity or social flexibility evolves
 289 in varying environments would then depend on the predictability of this variation. For
 290 developmental plasticity, the environment in which an individual grows up must contain
 291 reliable (predictable) information about the environment in which it will breed. In this case,
 292 the individual could develop an alternative phenotype via developmental plasticity with the
 293 highest reproductive success occurring in the future environment.

294 **Table 1**

295 Environmental conditions under which the four mechanisms leading to IVSO are predicted to
 296 evolve. Predictability can occur within generations (i.e., early and later life of an individual)
 297 or between generations (i.e., conditions experienced by adults and their offspring).

Mechanisms for IVSO	Environmental conditions under which it is predicted to evolve
Environmental disrupter	It is not an evolved trait but enforced and thus occurs in all environments
Genetic differentiation	Environmental variation between populations. Environment is predictable for the individual.
Developmental plasticity	Re-occurring variation within populations which the individuals can predict.
Social flexibility	Non-predictable but re-occurring variation within populations.

298

299 If the environment is not predictable but differs significantly from generation to
300 generation, social flexibility enabling an adaptive response at a later life history stage and not
301 during early development should evolve. Social flexibility offers the potential to respond
302 immediately in a number of ways to changing environmental conditions. In most cases of
303 developmental plasticity, such as a response to prevailing predation pressure (Steiner &
304 Buskirk 2008; Lind et al. 2015), there is no or only a very short time lag between the reliable
305 information and the fitness benefit of the alternative phenotype. In contrast, the time lag
306 between the juvenile stage and the breeding stage is often much longer. This could explain
307 why many examples exist of social flexibility explaining IVSO, but not for developmental
308 plasticity (Schradin, 2013). We therefore predict that developmental plasticity as the
309 mechanism for IVSO is most likely to occur in species where the juvenile and the breeding
310 life history stage follow shortly after one another. For example, in common voles (*Microtus*
311 *arvalis*), precocious fertile mating of non-weaned 14 days old females occurs (Tkadlec &
312 Zejda 1995), being an extreme example of overlap between the juvenile and the breeding
313 stage. Future studies will have to test whether developmental plasticity is the mechanism
314 leading to IVSO in some species and whether this is related to a short time lag between
315 development and reproduction. In sum, all three adaptive mechanisms leading to IVSO are
316 predicted to have evolved as a response to environmental variation (Table 1).

317

318 **Testing predictions at the species level**

319 Testing for the adaptive value of IVSO requires a comparison of the fitness of
320 individuals living in different types of social organizations under different environmental
321 conditions. For example, male striped mice have alternative reproductive tactics, being either
322 the breeding males of communally breeding groups (called breeding males) or solitary
323 roamers attempting to copulate with females of several groups (Schradin et al. 2009). In

324 striped mice, IVSO occurs within populations. Striped mice of both sexes live solitarily when
325 population density is low, but live in communally breeding groups when population density is
326 high. However, solitary roaming males occur even under high population densities (because
327 the sex ratio at birth is equal but there is only one breeding male per communal group), but
328 have a lower body mass (= competitive ability) than breeding males (Schradin et al. 2009).
329 Breeding males have 10 times higher reproductive success than roamers (Schradin &
330 Lindholm 2011). However, when only roaming males occur, many of them have very high
331 reproductive success (Schradin & Lindholm 2011). Importantly, under intermediate
332 population density, males (and also females) can be solitary or group-living, and the
333 reproductive success of roamers equals the reproductive success of breeding males (Schradin
334 & Lindholm 2011). This indicates that IVSO in this species is the result of selection having
335 acted on individuals to maximize reproductive success.

336 If adaptive IVSO has been identified in a species, the main expectation would be that
337 the species showing IVSO lives in a variable environment (Table 1). In striped mice,
338 population density is the main predictor of social organization, determining whether
339 individuals live in groups or solitarily (Schradin et al. 2010; Schoepf & Schradin 2012).
340 Population density is highly variable from year to year. This indicates that African striped
341 mice live in a variable and unpredictable environment, favoring the evolution of social
342 flexibility.

343 Statistically testing whether or not IVSO in a single species is due the variability in its
344 environment can be challenging. If genetic differentiation has been identified as the
345 mechanism of IVSO, one could measure selected environmental factors and compare these
346 between populations with social organization type A with populations showing the different
347 social organization type B. For this, an appropriate sample size is needed in the different
348 populations showing the two forms of social organization. If the identified mechanism is

349 developmental plasticity, it could be shown statistically that the environmental factors are
350 predictable for the individuals by doing autocorrelations or other time series analyses.

351 Social flexibility is characterized by environmental factors that are unpredictable, such
352 that no significant autocorrelation of the factors determining social organization would be
353 expected. For example, the population density experienced as juveniles would not predict
354 (correlate with) the population density when the individual is breeding. Thus, the
355 environmental factor measured at time_(breeding-x) does not predict the same factor at time_(breeding),
356 which would be the case if an identified cycle (for example 7 years) does not correspond with
357 the life history cycle (e.g. 2 year) of a species, or if no cycles exist at all, indicating
358 environmental unpredictability that results in non-significant statistical relationships. This
359 would be statistically problematic as one would expect the null hypothesis to be true (the
360 variable factor cannot be predicted). There are no tests demonstrating unpredictability, but
361 there are statistical tools such as time series tests to detect structure in a dataset. This can be
362 applied to a time series of environmental data and the absence of any signal at the time scales
363 of the animal's lifetime would indicate that the variable is unpredictable for the individual of
364 this study period. Potential methods include wavelet analysis which generates complementary
365 wavelets with different periodicities to decompose data without gaps. The wavelets are then
366 used to detect periodicity in the environmental time series at different time scales. Another
367 approach is to use a test for autocorrelation (Moran's test, Portmanteau test's, Box-Pierce,
368 Ljung-Box Q test) to detect a structure in the time series (Diggle 1990).

369

370 **Testing predictions in comparative studies**

371 The comparative method relies on large datasets of many species. Comparative studies
372 could be used to establish whether variation in key environmental factors such as rainfall and
373 food availability or life history are associated with the occurrence of IVSO over a large
374 number of species. There are three important issues we want to address about how to improve

375 future comparative studies. First, despite evidence that IVSO has been observed in mammals
376 (Dalerum 2007; Valomy et al. 2015; Garber et al. 2016; Mann & Karniski 2017), existing
377 databases on the social organization of mammals and other taxa typically do not consider
378 IVSO but assign one form of social organization to each species. Ignoring IVSO in
379 comparative studies can lead to spurious conclusions about social evolution (Silvestro et al.
380 2015; Sandel et al. 2016). For example, it was previously believed that social carnivores
381 evolved from a solitary ancestor, but taking IVSO into account indicated that the ancestor
382 might rather have been socially flexible (Dalerum 2007). Thus, it is crucial that IVSO is
383 considered in comparative studies of factors influencing social diversity in animals.

384 Second, to achieve maximum taxonomic breadth, some databases are populated with
385 information from the secondary literature and some data are based on the assumption that
386 closely related species have the same form of social organization, even if only one species has
387 been studied in detail. We advocate for a different approach in which scientists build a smaller
388 dataset based on the most reliable information from the primary literature (Schradin 2017) and
389 that includes IVSO (Valomy et al. 2015). Conclusions from comparative studies using high
390 quality primary data can differ significantly from comparative studies of large databases of
391 low quality data from the secondary and tertiary literature (Kappeler & Fichtel 2016). For
392 example, one database for comparative studies included 90% (399/445) of Eulipotyphla in their
393 dataset with >99% assigned a solitary social organization, often based on secondary literature
394 (Lukas & Clutton-Brock 2013). In contrast, Valomy et al. (2015) using only primary literature
395 determined that reliable information was only available for 16 species, of which 56% of
396 species (n=9/16) were social (living in pairs or in groups). Interestingly, IVSO was found in 7
397 Eulipotyphla species (Valomy et al. 2015). Detailed long-term studies can change our
398 understanding animal social systems even in well studied taxa (Elbroch et al. 2017).
399 Databases used in future comparative studies of IVSO and social evolution should be built
400 from data collected from the primary literature and not include assumptions about the social

401 organization of an entire genus based on observations in a single or a few species (Schradin
 402 2017). This will require that the social organizations of more species are studied in their
 403 natural environment (Valomy et al. 2015; Schradin 2017).

404 Third, the next major challenge with comparative studies is the restriction of analyses
 405 to adaptive forms of IVSO. This is difficult because environmental disrupters are a frequent
 406 cause of non-adaptive IVSO. Thus, it would be beneficial if databases on the social
 407 organization of a taxon do not only include whether IVSO occurs, but also whether it is
 408 adaptive or non-adaptive. Unfortunately, this information is normally not available.

409

410 **Predictions about the factors favouring the evolution of adaptive IVSO**

411 **Table 2**

412 Predictions regarding IVSO to be tested in comparative studies.

Hypothesis	Prediction & mechanisms
Non-adaptive	IVSO is more common in species that are typically characterised by one dominant breeding pair, indicating that environmental disrupters (death of one dominant breeder) cause the observed variation.
Benefits under environmental heterogeneity	IVSO occurs more frequently in species that occur in areas of the world characterized by high inter-annual (among) year variation (coefficient of variation) in rainfall and ambient temperature. This can for example induce significant variation in population density and thus competition for reproduction (and resources). A positive relationship between IVSO and increasing diet breadth and greater IVSO is expected in species found in regions with high within-year and inter-annual variation in rainfall and food availability.
Benefits to short lived species	IVSO is more common in species with a short lifespan and that breed only for one breeding season; these species are selected to respond optimally to the prevailing environmental situation.
Responsiveness to changing environments over a long lifetime	IVSO is greater in species with long lifespans and that reproduce during multiple years than species with short lifespans and that do not produce offspring during multiple breeding seasons and that IVSO is positively associated with habitat breadth.

413

414 The main prediction is that environmental factors important for fitness vary more in species
415 with than without IVSO (Table 2). Important factors are variation in rainfall and food
416 availability, which influence population density. Population density in combination with
417 resource availability can influence both the degree of competition within populations and the
418 extent to which ecological constraints limit reproductive and social options (Emlen 1982;
419 Koenig et al. 1992; Schradin 2013). Other environmental factors such as ambient temperature
420 and changes in predation pressure or parasite / infectious disease prevalence could also be
421 important for the evolution of IVSO.

422 The adaptive value of IVSO may depend on both environmental conditions and life
423 history (Table 2). This is expected when environmental variation has different effects on long-
424 lived versus short-lived species and those with many versus few breeding attempts during a
425 lifetime. Short-lived species will experience less environmental variation during a lifetime
426 and thus must breed in the prevailing environment rather than wait to breed until the
427 environmental conditions have improved. If an individual of a short-lived species chooses a
428 reproductive and social tactic that leads to a comparatively low reproductive success during
429 its only breeding opportunity, its lifetime reproductive success will be below average. In
430 contrast, an individual of a long-lived species that breeds during many breeding seasons can
431 have a relatively high lifetime reproductive success even if its tactic leads to low success in
432 one breeding season. As an extreme example, consider a reproductive tactic that leads to very
433 high reproductive success during years in which multiple preferred foods are abundant but to
434 no reproductive success in years when food availability is restricted. In a long-lived species
435 where individuals breed in many years, this reproductive tactic could still be advantageous.
436 However, in a short-lived species where every generation breeds for only one year and is then
437 replaced by the next generation, individuals with this reproductive tactic would die without
438 having reproduced, resulting in a shift in the frequency of an alternative tactic. In sum, we
439 predict that IVSO is more likely to evolve in short-lived species, particularly species where

440 individuals only breed during one single breeding season. This prediction should be compared
441 to the alternative prediction: long-lived species from heterogeneous environments evolved
442 IVSO as a tactic to cope with inter-annual variation in environmental conditions, thereby
443 using the best strategy for current conditions, while short-lived species are constrained to one
444 social tactic (Table 2).

445

446 **Conclusions**

447 The fact that a species shows IVSO is no evidence that it is an evolved trait of this species.
448 Environmental disrupters can be expected to cause IVSO even in species where IVSO is also
449 an adaptive response (Hill et al. 2015a; Hill et al. 2015b). Adaptive IVSO is expected to have
450 evolved in variable environments. To understand IVSO at the species level it is important to
451 conduct continuous long-term studies to differentiate between non-adaptive and adaptive
452 IVSO. In addition, it is necessary to measure variation in the environment, and statistical tools
453 such as time series analyses can be used test for structure in the data. One problem is that such
454 statistical analyses mainly demonstrate significant relationships such as cycles, but not non-
455 existing cycles, which would represent unpredictability. Thus, unpredictability is difficult to
456 demonstrate statistically, but an important factor for the evolution of social flexibility causing
457 IVSO.

458 IVSO is an important consideration when studying social evolution (evolution of
459 monogamy, cooperative breeding, paternal care, group versus solitary living), as not every
460 species can be assigned to one single form of social organization (Lott 1984; Lott 1991). For
461 such comparative studies, it is important to have reliable data based on the primary literature.
462 IVSO is an interesting phenomenon that needs scientific explanation. Understanding IVSO is
463 important because it demonstrates species resilience against environmental change and it can
464 help us to study ultimate and proximate reasons of group-living by comparing between
465 solitary and group-living individuals in a single species (Schradin et al. 2012). Finally, social

466 organization can influence both social structure and mating system, but does not determine
467 these. Thus, once adaptive IVSO has been identified, future studies should investigate its
468 effects on social structure and mating system.

469

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479 **Literature cited**

- 480 Auld, J. R., Agrawal, A. A. & Relyea, R. A. 2010: Re-evaluating the costs and limits of
481 adaptive phenotypic plasticity. *Proc. R. Soc. B-Biol. Sci.* **277**, 503-511.
- 482 Bendesky, A., Kwon, Y.-M., Lassance, J.-M., Lewarch, C. L., Yao, S., Peterson, B. K., He, M.
483 X., Dulac, C. & Hoekstra, H. E. 2017: The genetic basis of parental care evolution in
484 monogamous mice. *Nature* **544**, 434-439.
- 485 Berry, R. J., Tattersall, F. H. & Hurst, J. 2008: Genus *Mus*. In: *Mammals of the British Isles*
486 *Handbook*, 4th edn. (Harris, S. & Yalden, D. W., eds). The Mammal Society,
487 Southampton, U.K.
- 488 Burke, T., Davies, N. B., Bruford, M. W. & Hatchwell, B. J. 1989: Parental care and mating
489 behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA
490 fingerprinting. *Nature* **338**, 249-250.
- 491 Dalerum, F. 2007: Phylogenetic reconstruction of carnivore social organizations. *Journal of*
492 *Zoology* **273**, 90-97.
- 493 Davies, N. B. 1992: *Dunnock Behaviour and Social Evolution*. Oxford University Press,
494 Oxford.
- 495 Davies, N. B., Hartley, I. R., Hatchwell, B. J. & Langmore, N. E. 1996: Female control of
496 copulations to maximize male help: a comparison of polygynandrous alpine accentors,
497 *Prunella collaris*, and dunnocks, *P. modularis*. *Animal Behaviour* **51**, 27-47.
- 498 Dickman, C. R., Greenville, A. C., Beh, C.-L., Tamayo, B. & Wardle, G. M. 2010: Social
499 organization and movements of desert rodents during population “booms” and “busts”
500 in central Australia. *J. Mammal.* **91**, 798-810.
- 501 Diggle, P. J. 1990: *Time Series, A Biostatistical Introduction*. Clarendon Press, Oxford.

- 502 Dochtermann, N. A., Schwab, T. & Sih, A. 2015: The contribution of additive genetic
503 variation to personality variation: heritability of personality. *Proceedings of the Royal*
504 *Society B: Biological Sciences* **282**.
- 505 Ebensperger, L. A., Correa, L. A., León, C., Ramírez-Estrada, J., Abades, S., Villegas, Á. &
506 Hayes, L. D. 2016: The modulating role of group stability on fitness effects of group
507 size is different in females and males of a communally rearing rodent. *Journal of*
508 *Animal Ecology* **85**, 1502-1515.
- 509 Eggert, A.-K. 1992: Alternative male mate-finding tactics in burying beetles. *Behav Ecol* **3**,
510 243-254.
- 511 Elbroch, L. M., Levy, M., Lubell, M., Quigley, H. & Caragiulo, A. 2017: Adaptive social
512 strategies in a solitary carnivore. *Science Advances* **3**.
- 513 Emlen, S. T. 1982: The evolution of helping. I. An ecological constraints model. *Am Nat* **119**,
514 29-39.
- 515 Garber, P. A. 1997: One for all and breeding for one: cooperation and competition as a
516 tamarin reproductive strategy. *Evol Anthropol* **3**, 187-199.
- 517 Garber, P. A., Porter, L. M., Spross, J. & Di Fiore, A. 2016: Tamarins: Insights into
518 monogamous and non-monogamous single female social and breeding systems. *Am. J.*
519 *Primatol.* **78**, 298-314.
- 520 Gotzek, D. & Ross, K. G. 2007: Genetic regulation of colony social organization in fire ants:
521 An integrative overview. *Quarterly Review of Biology* **82**, 201-226.
- 522 -. 2009: Current Status of a Model System: The Gene Gp-9 and Its Association with Social
523 Organization in Fire Ants. *PLOS ONE* **4**.
- 524 Hayes, L. D. & Schradin, C. 2017: Long-term field studies in mammals: what the short-term
525 study cannot tell us. *J Mammal.*
- 526 Hill, D. L., Pillay, N. & Schradin, C. 2015a: Alternative reproductive tactics in female striped
527 mice: heavier females are more likely to breed solitarily than communally. *Journal of*
528 *Animal Ecology* **84**, 1497-1508.
- 529 -. 2015b: Alternative reproductive tactics in female striped mice: Solitary breeders have lower
530 corticosterone levels than communal breeders. *Horm. Behav.* **71**, 1-9.
- 531 Hofmann, H. A., Beery, A. K., Blumstein, D. T., Couzin, I. D., Earley, R. L., Hayes, L. D.,
532 Hurd, P. L., Lacey, E. A., Phelps, S. M., Solomon, N. G., Taborsky, M., Young, L. J.,
533 Rubenstein, D. R., Nescent Working Group on Integrative Models of Vertebrate
534 Sociality: Evolution, M. & Emergent, P. 2014: An evolutionary framework for
535 studying mechanisms of social behavior. *Trends in Ecology & Evolution* **29**, 581-589.
- 536 Hu, C. K. & Hoekstra, H. E. 2017: *Peromyscus* burrowing: A model system for behavioral
537 evolution. *Seminars in Cell and Developmental Biology* **61**, 107-114.
- 538 Judge, P. G. 2000: Coping with crowded conditions. In: *Natural conflict resolution*. (Aureli, F.
539 & De Waal, F., eds). University of California Press.
- 540 Kappeler, P. M. & Fichtel, C. 2016: The evolution of eulemur social organization.
541 *International Journal of Primatology* **37**, 10-28.
- 542 Kappeler, P. M. & Schaik, C. P. v. 2002: Evolution of primate social systems. *Int J Primatol*
543 **23**, 707-740.
- 544 Keller, L. 2009: Adaptation and the genetics of social behaviour. *Philos. Trans. R. Soc. Lond.*
545 *B. Biol. Sci.* **364**, 3209-3216.
- 546 Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L. & Stanback, M. T. 1992: The
547 evolution of delayed dispersal in cooperative breeders. *Quart Rev Biol* **67**, 111-150.
- 548 Latham, N. & Mason, G. 2004: From house mouse to mouse house: the behavioural biology
549 of free-living *Mus musculus* and its implications in the laboratory. *Applied Animal*
550 *Behaviour Science* **86**, 261-289.

- 551 Lind, M. I., Yarlett, K., Reger, J., Carter, M. J. & Beckerman, A. P. 2015: The alignment
552 between phenotypic plasticity, the major axis of genetic variation and the response to
553 selection. *Proceedings of the Royal Society of London B: Biological Sciences* **282**.
- 554 Lott, D. F. 1984: Intraspecific variation in the social systems of wild vertebrates. *Behaviour*
555 **88**, 266-325.
- 556 -. 1991: *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge
557 University Press, New York.
- 558 Löttker, P., Huck, M., Zinner, D. P. & Heymann, E. W. 2007: Grooming relationships
559 between breeding females and adult group members in cooperatively breeding
560 moustached tamarins (*Saguinus mystax*). *Am. J. Primatol.* **69**, 1159-1172.
- 561 Lukas, D. & Clutton-Brock, T. H. 2013: The evolution of social monogamy in mammals.
562 *Science* **341**, 526-530.
- 563 Mann, J. & Karniski, C. 2017: Diving beneath the surface: long-term studies of dolphins and
564 whales. *J. Mammal.* **98**, 621-630.
- 565 Markham, A. C. & Gesquiere, L. R. 2017: Costs and benefits of group living in primates: an
566 energetic perspective. *Philosophical Transactions of the Royal Society B: Biological*
567 *Sciences* **372**.
- 568 Martins, M. M., Nascimento, A. T., Nali, C., Velastin, G. O., Mangini, P. B., Valladares-
569 Padua, C. B. & Galetti Jr, P. M. 2015: A test for sex-biased dispersal in the black-
570 faced lion tamarin (*Leontopithecus caissara*): inferences from microsatellite markers.
571 *Studies on Neotropical Fauna and Environment* **50**, 14-20.
- 572 Mayer, M., Künzel, F., Zedrosser, A. & Rosell, F. 2017: The 7-year itch: non-adaptive mate
573 change in the Eurasian beaver. *Behav Ecol Sociobiol* **71**, 32.
- 574 Meynard, C. N., Pillay, N., Perrigault, M., Caminade, P. & Ganem, G. 2012: Evidence of
575 environmental niche differentiation in the striped mouse (*Rhabdomys sp.*): inference
576 from its current distribution in southern Africa. *Ecology and Evolution* **2**, 1008-1023.
- 577 Milleret, C., Wabakken, P., Liberg, O., Åkesson, M., Flagstad, Ø., Andreassen, H. P. & Sand,
578 H. 2017: Let's stay together? Intrinsic and extrinsic factors involved in pair bond
579 dissolution in a recolonizing wolf population. *Journal of Animal Ecology* **86**, 43-54.
- 580 Müller, J. F., Braunisch, V., Hwang, W. & Eggert, A.-K. 2006: Alternative tactics and
581 individual reproductive success in natural associations of the burying beetle,
582 *Nicrophorus vespilloides*. *Behav Ecol* **18**, 196-203.
- 583 Nonaka, E., Svanbäck, R., Thibert-Plante, X., Englund, G. & Brännström, Å. 2015:
584 Mechanisms by which phenotypic plasticity affects adaptive divergence and
585 ecological speciation. *The American Naturalist* **186**, E126-E143.
- 586 Ometto, L., Shoemaker, D., Ross, K. G. & Keller, L. 2011: Evolution of Gene Expression in
587 Fire Ants: The Effects of Developmental Stage, Caste, and Species. *Mol. Biol. Evol.*
588 **28**, 1381-1392.
- 589 Phoenix, C. H., Goy, R. W., Gerall, A. A. & Young, W. C. 1959: Organizing action of
590 prenatally administered testosterone propionate on the tissue mediating mating
591 behavior in the female guinea pig. *Endocrinology* **65**, 369-382.
- 592 Piersma, T. & Drent, J. 2003: Phenotypic flexibility and the evolution of organismal design.
593 *Trends in Ecology & Evolution* **18**, 228-233.
- 594 Piersma, T. & Gils, J. A. v. 2011: *The flexible Phenotype*. Oxford University Press, Oxford.
- 595 Porter, L. M., Hanson, A. M. & Becerra, E. N. 2001: Group demographics and dispersal in a
596 wild group of Goeldi's monkeys (*Callimico goeldii*). *Folia Primatol* **72**, 108-110.
- 597 Randall, J. A., Rogovin, K., Parker, P. G. & Eimes, J. A. 2005: Flexible social structure of a
598 desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints.
599 *Behav Ecol* **16**, 961-973.
- 600 Reyer, H.-U. 1984: Investment and relatedness: a cost/benefit analysis of breeding and
601 helping in the pied kingfisher (*Ceryle rudis*). *Anim. Behav.* **32**, 1163-1178.

- 602 Reyer, H. U. 1980: Flexible helper structure as an ecological adaptation in the pied kingfisher
603 (*Ceryle rudis rudis* L.). *Behav Ecol Sociobiol* **6**, 219-227.
- 604 Rymer, T., Pillay, N. & Schradin, C. 2013: Extinction or survival? Behavioral flexibility in
605 response to environmental change in the African striped mouse *Rhabdomys*.
606 *Sustainability* **5**, 163-186.
- 607 Sandel, A. A., Miller, J. A., Mitani, J. C., Nunn, C. L., Patterson, S. K. & Garamszegi, L. Z.
608 2016: Assessing sources of error in comparative analyses of primate behavior:
609 Intraspecific variation in group size and the social brain hypothesis. *Journal of Human*
610 *Evolution* **94**, 126-133.
- 611 Schoepf, I. & Schradin, C. 2012: Better off alone! Reproductive competition and ecological
612 constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*).
613 *Journal of Animal Ecology* **81**, 649-656.
- 614 Schradin, C. 2013: Intraspecific variation in social organization by genetic variation,
615 developmental plasticity, social flexibility or entirely extrinsic factors. *Philos. Trans.*
616 *R. Soc. B-Biol. Sci.* **368**.
- 617 Schradin, C. 2017: Comparative studies need to rely both on sound natural history data and on
618 excellent statistical analysis. *R. Soc. Open Sci.* .
- 619 Schradin, C. & Hayes, L. D. 2017: A synopsis of long-term field studies in mammals:
620 achievements, future directions, and some advice *J Mammal*.
- 621 Schradin, C., König, B. & Pillay, N. 2010: Reproductive competition favours solitary living
622 while ecological constraints impose group-living in African striped mice. *Journal of*
623 *Animal Ecology* **79**, 515-521.
- 624 Schradin, C. & Lindholm, A. K. 2011: Relative fitness of alternative male reproductive tactics
625 in a mammal varies between years. *Journal of Animal Ecology* **80**, 908-917.
- 626 Schradin, C., Lindholm, A. K., Johannesen, J., Schoepf, I., Yuen, C.-H., König, B. & Pillay,
627 N. 2012: Social flexibility and social evolution in mammals: a case study of the
628 African striped mouse (*Rhabdomys pumilio*). *Molecular Ecology* **21**, 541-553.
- 629 Schradin, C., Scantlebury, M., Pillay, N. & König, B. 2009: Testosterone levels in dominant
630 sociable males are lower than in solitary roamers: physiological differences between
631 three male reproductive tactics in a sociably flexible mammal. *Am Nat* **173**, 376-388.
- 632 Shultz, S., Opie, C. & Atkinson, Q. D. 2011: Stepwise evolution of stable sociality in
633 primates. *Nature* **479**, 219-222.
- 634 Silvestro, D., Kostikova, A., Litsios, G., Pearman, P. & Salamin, N. 2015: Measurement
635 errors should always be incorporated in phylogenetic comparative analysis. *Methods*
636 *of Ecol Evol* **6**, 340-346.
- 637 Steiner, U. K. & Buskirk, J. V. 2008: Environmental stress and the costs of whole-organism
638 phenotypic plasticity in tadpoles. *J. Evol. Biol* **21**, 97- 103.
- 639 Tinbergen, N. 1963: On aims and methods of ethology. *Z Tierpsychol* **20**, 410-433.
- 640 Tkadlec, E. & Zejda, J. 1995: Precocious Breeding in Female Common Voles and Its
641 Relevance to Rodent Fluctuations. *Oikos* **73**, 231-236.
- 642 Valomy, M., Hayes, L. D. & Schradin, C. 2015: Social organization in Eulipotyphla: evidence
643 for a social shrew. *Biology Letters* **11**.
- 644 VanBuskirk, J. & Steiner, U. K. 2009: The fitness costs of developmental canalization and
645 plasticity. *J. Evol. Biol* **22**, 852- 860.
- 646 West-Eberhard, M. J. 2003: *Developmental Plasticity and Evolution*. Oxford University Press,
647 Oxford.
- 648 Zabel, C. J. & Taggart, S. J. 1989: Shift in red fox, *Vulpes vulpes*, mating system associated
649 with El Niño in the Bering Sea. *Animal Behaviour* **38**, 830-838.
- 650 Zimmermann, T. D., Kaiser, S., Hennessy, M. B. & Sachser, N. 2017: Adaptive shaping of
651 the behavioural and neuroendocrine phenotype during adolescence. *Proceedings of the*
652 *Royal Society B: Biological Sciences* **284**.

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654